

A NEW SPECIES OF *SCOLELEPIS* (POLYCHAETA: SPIONIDAE), HIGHLY ABUNDANT ON THE SAND BEACHES OF WESTERN PHUKET ISLAND, THAILAND

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ABSTRACT

Scoelepis (Scoelepis) laciniata n. sp. is described from the intertidal zone of sandy beaches along the west coast of Phuket Island, Thailand. It belongs to the group of species that lacks notopodia on the first setiger and lacks hooded hooks in all notopodia. The most striking character of the new species is the presence of 3–5 lateral fringes on the notopodial postsetal lamellae of anteriormost middle setigers. Furthermore, on most of these setigers 1–5 terminal and subterminal, clavate papillae are present on the branchiae. Ciliation on the palps is strongly reduced. During the height of the southwest monsoon season (especially July to October), the new species is the dominant element within the macrofauna of the intertidal zone just above median tide level. *Scoelepis* (S.) *laciniata* appears to be particularly plentiful at more protected sites.

Very little is known about the spionid fauna of Thailand. In a study of distribution patterns among spionids from depths of 10–30 m off the west coast of Phuket Island, Hylleberg and Nateewathana (1991a) reported the presence of about 38 species. The majority of these species belonged to *Prionospio* sensu lato, eight of which were described in a later publication (Hylleberg and Nateewathana 1991b). The presence of *Scoelepis* was also mentioned in the former of these papers, but no details were provided. No named species of *Scoelepis* have previously been reported from Thailand, although considerable information does exist from adjacent Indo-Pacific areas (de Silva 1961, 1965; Blake and Kudenov 1978; Hutchings and Turvey 1984).

The material reported on in this paper was originally collected by Dr Deborah M. Dexter (San Diego State University) in connection with an investigation of the community structure of sandy beaches along the west coast of Phuket Island, Thailand. Over the course of 1 year (June 1994 to May 1995), monthly samples were taken at selected beaches, the quantitatively most important ones being, from north to south, Nai Yang (also known as Bang Tao), Patong, Kata, and Nai Harn (just north of Prom Thep). A map showing the collection sites will be published by Dexter; other maps are available in the literature, e.g., in Hylleberg, Nateewathana and Bussarawit 1986. Animals were sorted and given a preliminary name before being sent to the present author for confirmation and/or more detailed identification.

Further study of over 4,100 specimens labelled as “Spionidae sp. #1” revealed that at least five species of *Scoelepis* were present, two of them in very high numbers. One of the less common species was represented by 12 individuals of *Scoelepis (Scoelepis) lingulata* Imajima, 1992, originally described from Honshu Island, Japan (new record for Thailand). The four other species all appear to be undescribed, including the one which occurred in greatest numbers. At three of the four principal study beaches, this species completely dominated the fauna of sand flats just above median tide level during a significant part of the year. This species is described below.

MATERIALS AND METHODS

In collecting the material on which this paper reports, Dexter used a stratified random sampling design in which each beach was divided into four zones according to parameters such as appearance, slope, and the length of time exposed to air. From the water's edge, these four zones are referred to as the zone of saturation, zone of resurgence, zone of retention, and zone of drying sand. In each of them, five sites were selected at random and sampled using a stainless steel core with a surface area of 0.01 m², pushed to a depth of 10 cm. Animals were washed from the sand using a 500- μ m mesh sieve and fixed in formalin. Further details on these sampling methods may be found in Dexter (1990, 1992).

The material was transferred to alcohol upon receipt in Copenhagen. To provide illustrations of parapodia and setae, a paratype similar in size to, and of the same sex as, the holotype (i.e., a mature male) was chosen from the type sample. Parapodia from 13 setigers were mounted and embedded in euparal, most of them in anterior as well as posterior view (ZMUC-POL-431). Parapodia and setae were observed using differential interference contrast (Nomarski) microscopy. Drawings were made using a camera lucida attached to either a Wild M5 or a Zeiss Axioskop microscope.

Animals chosen for SEM were critical point dried, sputter-coated with gold, and studied in a JEOL JSM-840 scanning electron microscope. Probably due to defective sonication equipment, several attempts to remove the hoods from the hooded hooks (following the method described by Nishino and Ohwada 1991) were unsuccessful. Therefore, the number of accessory teeth above the main fang of these hooks could only be determined using light microscopic methods.

Type material has been deposited at the following institutions: Phuket Marine Biological Centre, Phuket, Thailand (PMBC); Zoological Museum, University of Copenhagen, Denmark (ZMUC); Australian Museum, Sydney (AM); Natural History Museum, London (BMNH); Natural History Museum of Los Angeles County, Los Angeles (LACM-AHF); Canadian Museum of Nature, Ottawa (CMNA); National Museum of Wales, Cardiff (NMW); Swedish Museum of Natural History, Stockholm (SMNH); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Scoelepis (Scoelepis) laciniata new species

Figures 1–6

Diagnosis.—A member of *Scoelepis (Scoelepis)* lacking notopodial hooded hooks and lacking notosetae on setiger 1; prostomium without occipital antenna or obvious caruncle, with 2 pairs of small eyes; peristomium closely apposed to prostomium, without lateral wings; palps with transverse rows of cilia arranged in a single band; gills on number of anterior and middle setigers (usually setigers 15–26) with 1–5 terminal and subterminal, clavate papillae; neuropodial postsetal lamella divided into 2 lobes from about setiger 18 to end of body; notopodial postsetal lamellae from about setiger 10 to about setiger 26 with 1–5 lateral lobes, giving them a fringed appearance; hooded hooks bidentate, with single large tooth surmounting main fang; pygidium appearing inflated, almost spherical.

Material Examined.—All specimens were collected by Dexter at beaches along the west coast of Phuket Island, Thailand.

Patong Beach (TYPE LOCALITY): June 20, 1994 (ZMUC-POL-430, 74 PARATYPES); July 26, 1994 (PMBC-11667, 374 PARATYPES); Aug. 16, 1994 (PMBC-11665, HOLOTYPE; PMBC-11666, 40 PARATYPES; ZMUC-POL-431, slide series of 1 PARATYPE; ZMUC-POL-432, SEM stubs of 3 PARATYPES; ZMUC-POL-433, 15 PARATYPES; AM, 15 PARATYPES; BMNH 1995.959-973, 15 PARATYPES; CMNA1995-0697, 15 PARATYPES; LACM-AHF POLY 1722, 15 PARATYPES; NMW.Z.1995.053, 15 PARATYPES; SMNH-4786, 15 PARATYPES; USNM-170032, 15 PARATYPES); Aug. 25, 1994 (PMBC-11668, 53 PARATYPES); Sept. 22 (ZMUC-POL-434, 37 PARATYPES); Oct. 7, 1994 (PMBC-11669, 38 PARATYPES); Nov. 22, 1994 (ZMUC-POL-435, 21 PARATYPES); Dec. 6, 1994 (PMBC-11670, 26 PARATYPES); Jan. 2, 1995 (ZMUC-POL-436, 13 PARATYPES); Feb. 6, 1995 (PMBC-11671, 24 PARATYPES); Mar. 3, 1995 (ZMUC-POL-437, 24 PARATYPES); Apr. 3, 1995 (PMBC-11672, 4 PARATYPES); May 1, 1995 (ZMUC-POL-438, 1 PARATYPE).

Kata Beach: June 24, 1994 (PMBC-11673, 68 specimens); Aug. 10, 1994 (ZMUC-POL-439, 297 spec.); Sept. 9, 1994 (PMBC-11674, 308 spec.); Oct. 6, 1994 (ZMUC-POL-440, 221 spec.); Nov. 3, 1994 (PMBC-11675, 17 spec.); Dec. 3, 1994 (ZMUC-POL-441, 174 spec.); Jan. 4, 1995 (PMBC-11676, 7 spec.); Feb. 4, 1995 (ZMUC-POL-442, 3 spec.); Mar. 4, 1995 (PMBC-11677, 66 spec.); Apr. 1, 1995 (ZMUC-POL-443, 9 spec.); May 2, 1995 (PMBC-11678, 2 spec.).

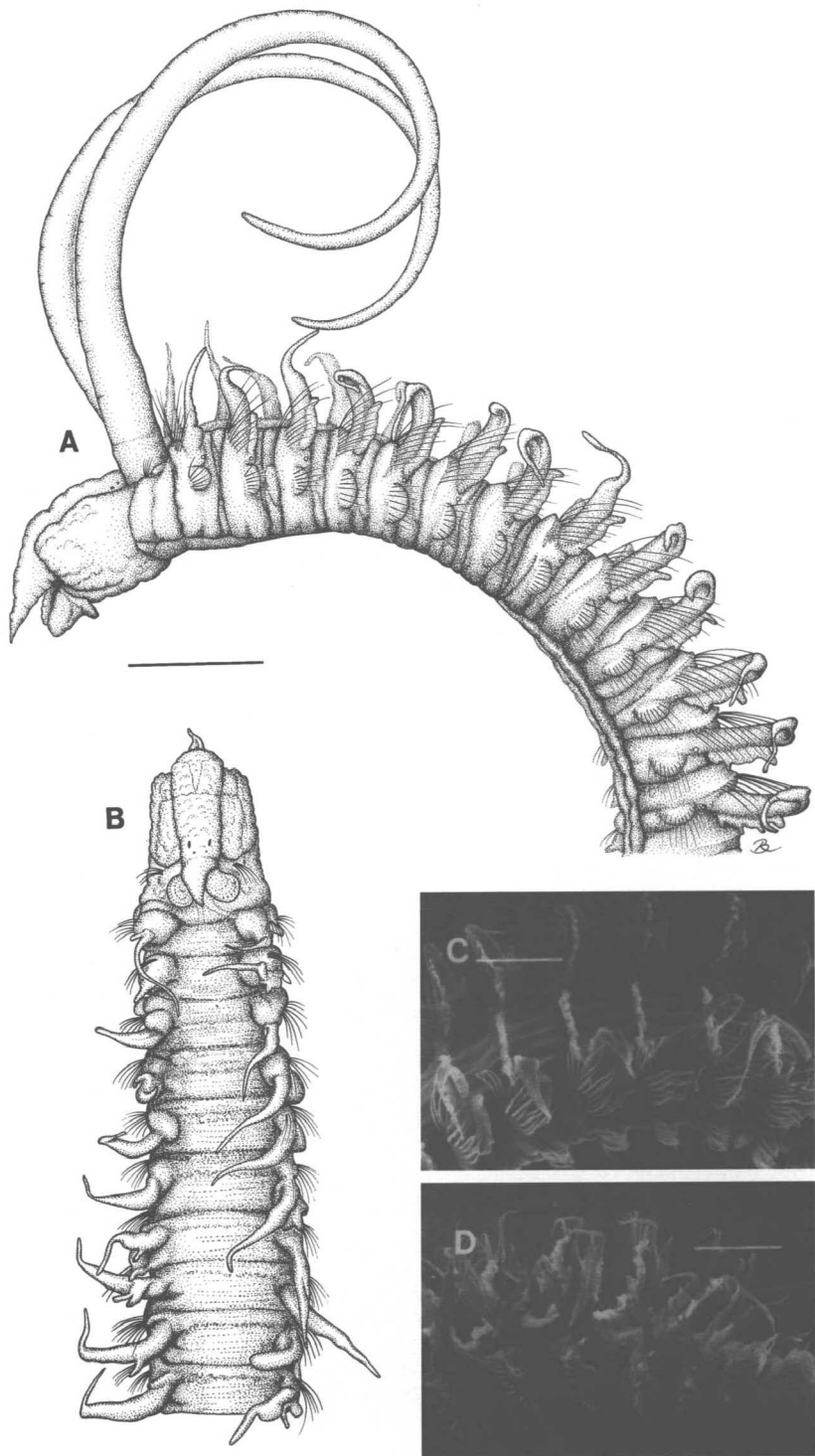


Figure 1. *Scololepis* (*S.*) *laciniata*. A: Lateral view of anterior end, holotype. B: Dorsal view of anterior end, paratype with palps removed (ZMUC-POL-433). C: Dorsolateral view of setigers 8–13 (anterior end to the left). D: Lateral view of posterior segments and pygidium. C and D are SEM micrographs of specimens from ZMUC-POL-444. Scale = 0.5 mm for drawings (A, B) and 0.25 mm for micrographs (C, D).

Nai Harn Beach: Sept. 21, 1994 (ZMUC-POL-444, SEM stubs of 4 spec.; ZMUC-POL-445, 49 spec.); Oct. 5, 1994 (PMBC-11679, 225 spec.); Nov. 1, 1994 (ZMUC-POL-446, 134 spec.); Dec. 2, 1994 (PMBC-11680, 59 spec.); Jan. 3, 1995 (ZMUC-POL-447, 48 spec.); Feb. 3, 1995 (PMBC-11681, 28 spec.); Mar. 1, 1995 (ZMUC-POL-448, 80 spec.); Apr. 2, 1995 (PMBC-11682, 29 spec.).

Nai Yang Beach: June 22, 1994 (PMBC-11683, 50 spec.); Mar. 6, 1995 (PMBC-11684, 1 spec.).

Naithon Beach: Oct. 4, 1994 (PMBC-11685, 1 spec.).

Karon Beach: Sept. 9, 1994 (PMBC-11686, 6 spec.).

Description.—Holotype a mature male, complete with 65 setigers; 17.5 mm long and up to 0.9 mm broad, excluding setae. Other specimens up to 19.0 mm long, with a maximum of 66 setigers (ZMUC-POL-434); samples also containing juveniles only 2.0 mm long and having as few as 20 setigers. Middle and posterior segments more elongate than anterior ones. Body almost rectangular in cross section. Preserved animals generally pale, with medioventral band of reddish brown pigment starting on peristomium and continuing on variable number of anterior segments. Juvenile animals (up to a length of about 8 mm) with transverse brown markings on dorsum of anterior segments. Living animals pale apart from red blood vessels in gills and grass-green pigment on anterior part of venter, continuing dorsolaterally on setigers 1 and 2 and also as a narrow, posterior longitudinal band on each palp; very faint, darker, transverse markings may be present on dorsum of anterior setigers.

Anterior end of prostomium acute, pointing forward and somewhat downwards (Fig. 1A; 2A); posterior end of prostomium also acute, slightly raised, without occipital antenna or obvious caruncle (Fig. 1B; 2B, C). Two small pairs of light reddish brown eyes present, anterior pair largest and slightly wider set (Fig. 1B). Peristomium enveloping prostomium and closely apposed to it, not forming lateral wings (Fig. 1B; 2C). Proboscis usually somewhat everted on preserved animals, densely covered with cilia (Fig. 2A, C). Palps slender and elongate, 3.4 mm long on holotype (Fig. 1A); with single longitudinal band comprised of 40 μ m long, transverse rows of cilia along anteromedial edge (Fig. 2C, D); this band does not extend to base of palp and is somewhat more obvious on juvenile individuals (i.e., palps more slender but band of same width as in adults); ciliary groove absent. Palp sheaths short, with smooth edge, and without special adornment (Fig. 2A). Nuchal organs heavily ciliated, crescent-shaped, at posteromedial base of palps (Fig. 2B).

Gills present from setiger 2 to end of body, longest on anterior and middle setigers; fused to notopodial postsetal lamellae but always with long terminal portion free (Figs 3–5). Each gill with well-developed, narrow band of cilia along inner edge, continuous with that of gill on other side of body; joined by narrow transverse band of cilia across dorsum, which on posterior setigers runs on dorsal edge of thin, elevated dorsal crest; ciliary band sometimes interrupted at base of gill (Fig. 1C, D). Clavate papillae present at tip of gill on number of anterior and middle setigers (Fig. 2E), beginning as 1 or 2 on setiger 15–16, rapidly increasing to 4 or 5 (Fig. 3J), thereafter decreasing in number, usually absent by setiger 28 (Fig. 4B).

Setiger 1 weakly developed; notopodium and notosetae completely absent; neuropodium with small, rounded postsetal lamella (Fig. 3A) and 3–4 short, limbate capillaries (Fig. 3B). Neuropodial postsetal lamella evenly rounded on following setigers (Fig. 3C, D), developing larger ventral lobe by setiger 5–7 (Fig. 3G); ventral lobe gradually becoming acute and separated from rest of lamella due to growing notch (Fig. 3H, I) on following setigers, completely divided into 2 separate, triangular lobes by setiger 17–18 (Fig. 3J); distance between dorsal and ventral lobes of neuropodial postsetal lamella increasing on subsequent setigers,

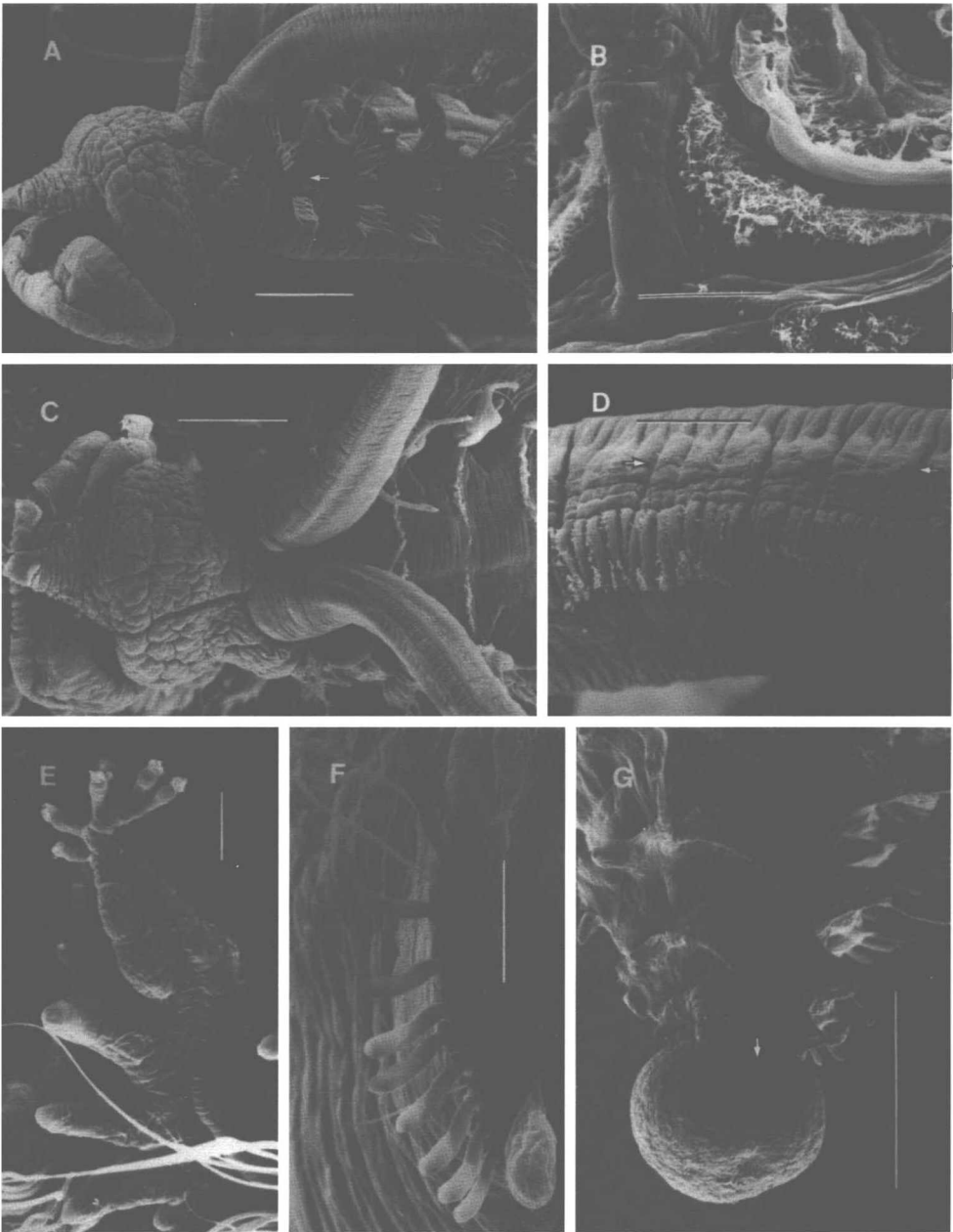


Figure 2. *Scololepis* (*S.*) *laciniata*. SEM micrographs. A: Anterior end, lateral view; interramal ciliated organ between neuro- and notopodium of second setiger indicated by arrow. B: Right nuchal organ of specimen in which palps have been removed; posterior tip of prostomium in upper left corner. C: Anterior end, dorsal view. D: Anterior view of middle section of palp, showing relatively short transverse rows of cilia; row of ciliated protuberances visible between arrows. E: Lateral view of gill and notopodial postsetal lamella from setiger 17, showing 5 clavate papillae at tip of gill. F: Lateral view of neuropodium from setiger 55; only part of dorsal lobe of neuropodial postsetal lamella visible. G: Dorsal view of posterior segments and pygidium, showing anal opening (arrow). ZMUC-POL-444 (A, C, E, F) and ZMUC-POL-432 (B, D, G). Scale = 0.25 mm (A, C, G) or 50 μ m (B, D-F).

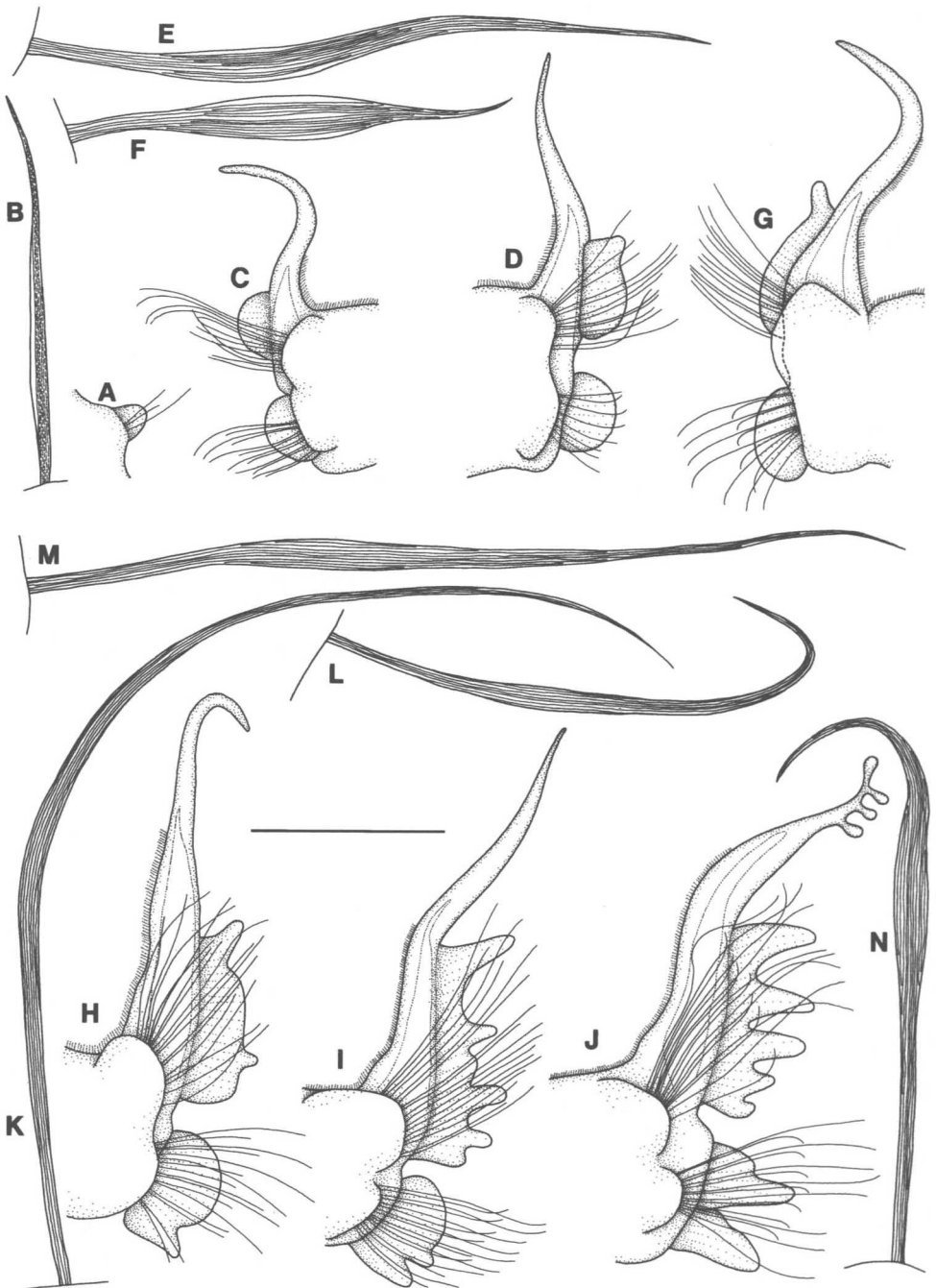


Figure 3. *Scolelepis* (*S.*) *laciniata*. Parapodia and setae from anterior setigers of paratype (ZMUC-POL-431). A: Parapodium (=neuropodium) of setiger 1. B: Neuroseta from setiger 1. C: Parapodium of setiger 2. D: Parapodium of setiger 3. E: Notoseta from setiger 3. F: Neuroseta from setiger 3. G: Parapodium of setiger 7. H: Parapodium of setiger 12. I: Parapodium of setiger 15. J: Parapodium of setiger 18. K: Posterior notoseta from setiger 18. L: Anterior notoseta from setiger 18. M: Posterior neuroseta from setiger 18. N: Anterior neuroseta from setiger 18. All parapodia shown in anterior view. Scale = 0.25 mm for all parapodia (A, C, D, G–J) and 50 μ m for all setae (B, E, F, K–N).

widely separated on posterior part of body (Fig. 5A, F), the lobes themselves becoming rounded or quadrangular (Fig. 4B, C, H; 5A), somewhat more pointed on last setigers (Fig. 5F).

First notopodial postsetal lamella on setiger 2, rounded (Fig. 3C), developing dorsolateral lobe on following setigers (Fig. 3D, G); a second, lateral lobe present by setiger 10–11 (Fig. 3H); further lateral lobes develop in quick succession on following setigers (Fig. 3I), 4–5 well-developed lobes being present by setiger 18 (Fig. 3J), lobes elongate triangular or somewhat digitate; lateral lobes become broader and shorter on subsequent setigers (Fig. 4A, B), no longer distinct by setiger 28 (Fig. 4C); dorsalmost and ventralmost lobes of notopodial postsetal lamellae generally persist on rest of body (Fig. 4H; 5A, F).

Neurosetae on anterior and middle setigers placed in 2 rows, on posterior setigers in 1 row, emerging from low, broad lobe; neuropodia of anterior setigers with capillaries only, those of anterior row subterminally broadest, weakly bilimbate (Fig. 3F, N), shorter than those of posterior row (Fig. 3M). Neuropodial hooded hooks first appearing on setiger 24–26 ($N = 55$), only 1 or 2 at first, slowly increasing to 9 or 10 on posterior setigers; hooded hook ending in bluntly rounded main fang, surmounted by single, somewhat shorter accessory tooth (Fig. 4G; 5H); in some cases, 2 very small, basal accessory teeth observed (Fig. 5C, D); hood with round, smooth-edged opening (Fig. 4G; 5C, D), more or less occluded on posterior setigers (Fig. 1D; 2F; 5H). From first appearance of hooded hooks, normal neurosetal capillaries become gradually replaced by maximum of 4 shorter, more slender companion setae (Fig. 1D; 2F; 4F; 5E, I). Well-developed interramal ciliated organ present between neuropodium and notopodium on all parapodia (Fig. 2A; 4H; 5F; not illustrated on all figures of parapodia), including above neuropodium of setiger 1, despite absence of notopodium.

Notosetae arranged in 2 rows in parapodia along entire body, emerging from somewhat elevated, rounded lobe; all notosetae capillaries, notopodial hooded hooks absent; capillaries of posterior row (Fig. 3K, 4D) always longer than those of corresponding anterior row (Fig. 3E, L; 4E); most notosetae weakly bilimbate, longest on middle setigers (Fig. 4D, E), gradually decreasing in length towards end of body (Fig. 5B, G).

Pygidium rounded, almost spherical (Fig. 2G), although somewhat broader ventrally than dorsally (Fig. 1D); anal opening at anterodorsal base of pygidium (Fig. 2G).

Sexually mature individuals with at least 60 setigers; sexual products limited to number of middle segments, usually setigers 18 to 42.

Tube very fragile, consisting of thin inner layer of mucus covered with tiny shell fragments, foraminiferans, and debris.

Etymology.—The species epithet *laciniata* (derived from the Latin noun *lacinia* = a flap or lobe) refers to the fringed appearance of the notopodial postsetal lamellae on the anteriormost middle setigers.

Distribution.—Known only from the intertidal zone of sandy beaches along the west coast of Phuket Island, Thailand. Future studies may demonstrate this species to be common at similar sites in the Andaman Sea region.

Taxonomic Remarks.—Maciolek (1987) divided *Scolecopsis* into two subgenera according to whether the hooded hooks were uni- to tridentate with a falcate or straight shaft (subgenus *Scolecopsis* de Blainville, 1828) or multidentate with a curved shaft (subgenus *Parascolecopsis* Maciolek, 1987). Furthermore, the latter have well-developed palpal sheaths; in *Scolecopsis* (*Scolecopsis*) they are short and

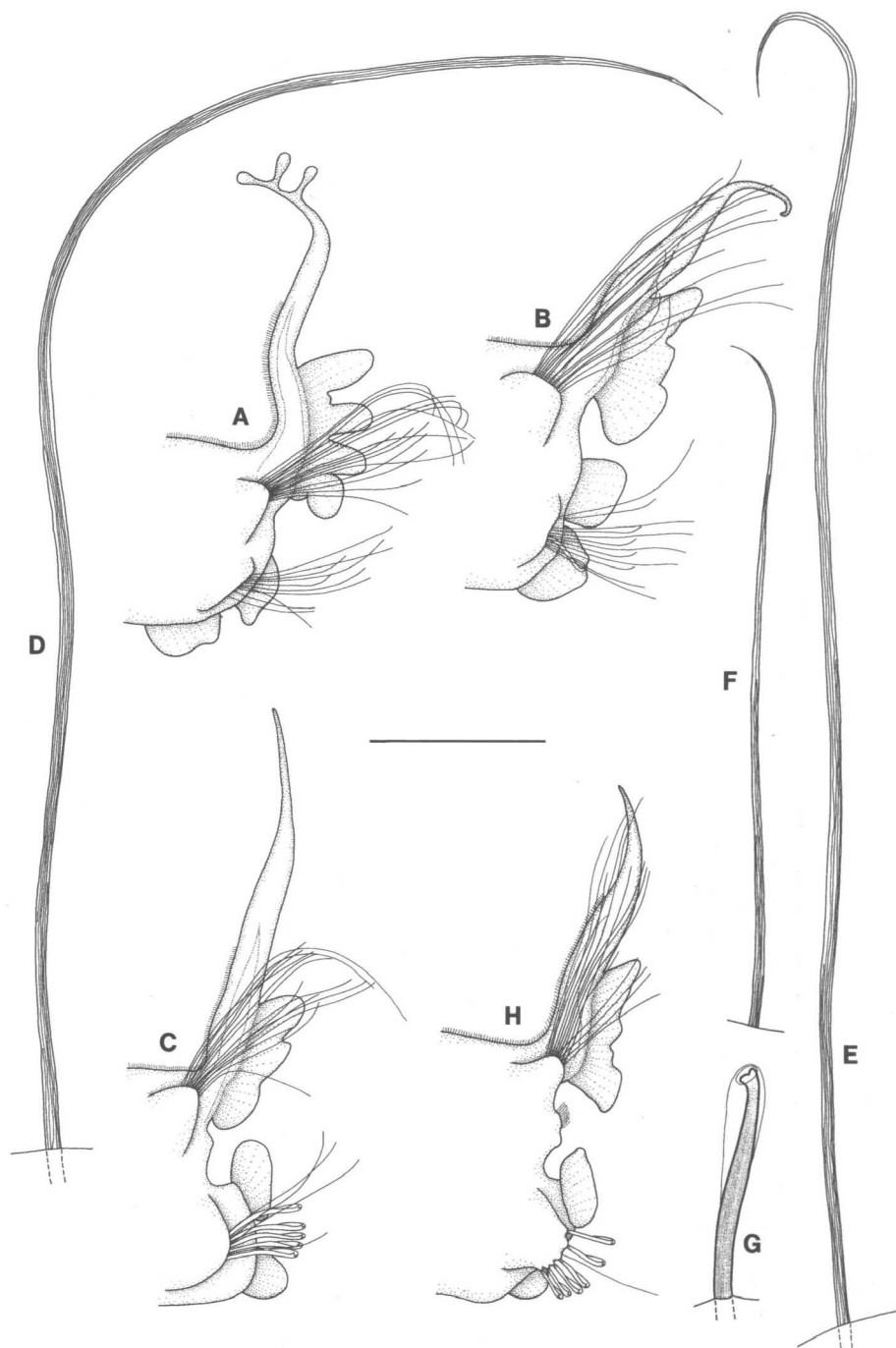


Figure 4. *Scoelepis* (*S.*) *laciniata*. Parapodia and setae from middle setigers of paratype (ZMUC-POL-431). A: Parapodium of setiger 21. B: Parapodium of setiger 24. C: Parapodium of setiger 28. D: Posterior notoseta from setiger 28. E: Anterior notoseta from setiger 28. F: Companion seta from neuropodium of setiger 28. G: Inferior hooded hook from neuropodium of setiger 28, lateral view. H: Parapodium of setiger 34. All parapodia shown in anterior view. Scale = 0.25 mm for all parapodia (A–C, H) and 50 μ m for all setae (D–G).

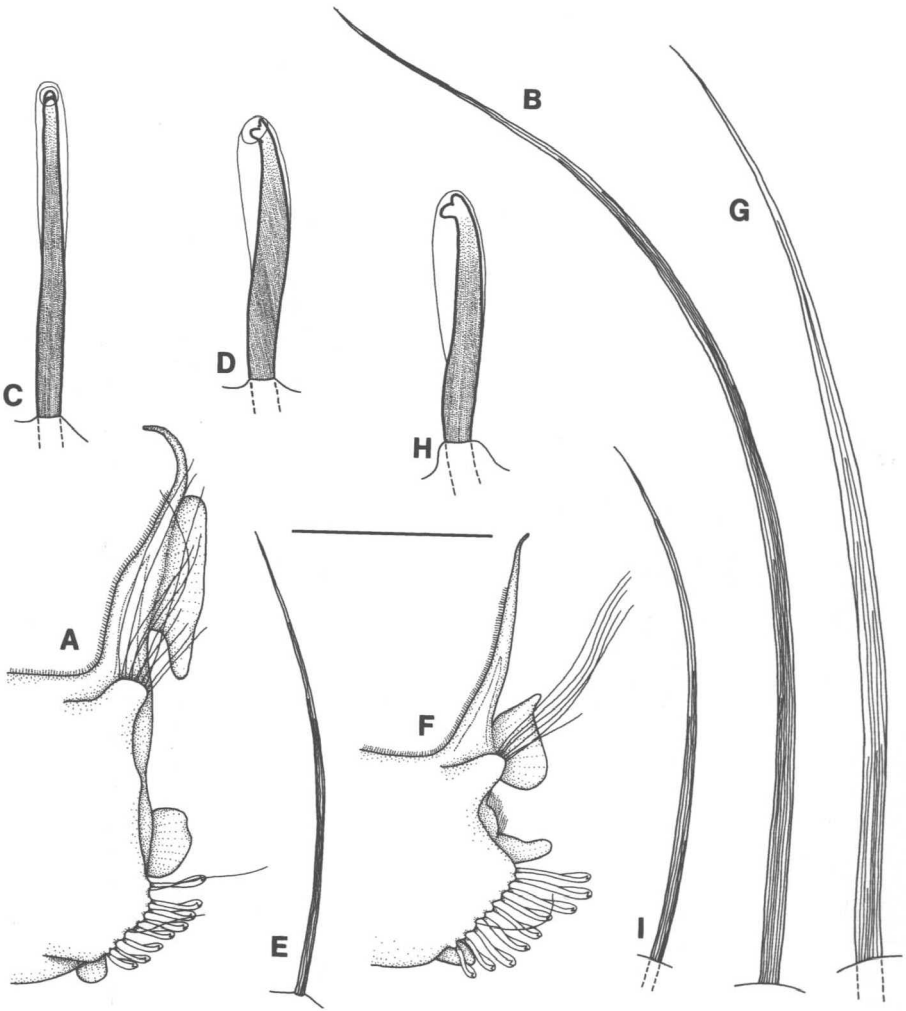


Figure 5. *Scolelepis (S.) laciniata*. Parapodia and setae from posterior setigers of paratype (ZMUC-POL-431). A: Parapodium of setiger 45. B: Notoseta from setiger 45. C: Superior hooded hook from neuropodium of setiger 45, dorsal view. D: Inferior hooded hook from neuropodium of setiger 45, lateral view. E: Companion seta from neuropodium of setiger 45. F: Parapodium of setiger 60. G: Notoseta from setiger 60. H: Inferior hooded hook from neuropodium of setiger 60, lateral view. I: Companion seta from neuropodium of setiger 60. Both parapodia shown in anterior view. Scale = 0.25 mm for parapodia (A, F) and 50 μ m for setae (B-E, G-I).

fused to the palp. On this basis, the new species is, for the time being, assigned to the subgenus *Scolelepis*. It is, however, highly likely that the hook morphology and palpal sheath development of this subgenus are plesiomorphic, being present also in *Dispia*, which is probably the sister taxon of *Scolelepis*. Thus, while *Scolelepis (Parascolelepis)* appears to be defined on the basis of good autapomorphies, *Scolelepis (Scolelepis)* may well be paraphyletic. Future revisions should focus on ascertaining whether an autapomorphic character can be found for the nominal subgenus.

Other species that lack notosetae on setiger 1 and hooded hooks on all notopodia are *S. (S.) cantabra* (Rioja, 1918), *S. (S.) williamsi* (de Silva, 1961), *S. (S.) aitutaki* Gibbs, 1972, *S. (S.) phyllobranchiata* Blake and Kudenov, 1978, *S. (S.)*

victoriensis Blake and Kudenov, 1978, *S. (S.) vexillatus* (Hutchings and Rainer, 1979), and *S. (S.) bullibranchiata* Rossi, 1982. However, with the exception of *S. (S.) williami* and *S. (S.) bullibranchiata* they all have notopodial postsetal lamellae on the anterior setigers that are completely fused with the gills to their tips. None of these 7 species display a laciniate pattern of prominent lateral lobes on the notopodial postsetal lamellae.

S. (S.) bullibranchiata differs from the species described here in having notopodial lamellae on setiger 1, tridentate hooded hooks, and a semicircular pygidium.

S. (S.) laciniata most closely resembles *S. (S.) williami* (de Silva, 1961) as only these two species in the genus are known to possess clavate papillae at the tip of some of their branchiae. De Silva's species (described from Sri Lanka) is, however, much larger than *S. (S.) laciniata* (up to 72 mm long), neuropodial hooded hooks begin posterior to setiger 40, pygidial morphology is very different, and the notopodial postsetal lobes are without laciniation.

The notopodial postsetal lamellae on anterior setigers of *S. (S.) carunculata* Blake and Kudenov, 1978 (described from Queensland, Australia) are greatly folded (like an accordion), resembling those of the anteriormost middle setigers in *S. (S.) laciniata*. The resemblance is, however, superficial (i.e., not two-dimensional) and *S. (S.) carunculata* has notosetae on setiger 1 and notopodial hooded hooks on posterior segments, denying any close relationship with the species described here.

The ciliation pattern on the palps of *S. (S.) laciniata* corresponds to that described for the genus by Dauer (1987) in that a ciliary groove is absent. However, in the two other species that have been studied (*S. (S.) squamata* (O. F. Müller, 1806) and *S. (S.) hutchingsae* Dauer, 1985) two bands of transverse rows are present, one of them being composed of somewhat longer, more closely set rows than the other (Dauer 1987; pers. obs.). The transverse rows of cilia on the palps of *S. (S.) laciniata* are longer (40 μm) than those of the short row in *S. (S.) squamata* (maximum length 33 μm according to Dauer 1987). Furthermore, in the new species the band of transverse rows of cilia on the palp is accompanied by a band of weakly ciliated protuberances running parallel to it (Fig. 2D). The spacing of these protuberances along the palp relative to that of the transverse rows strongly suggests that they represent the greatly reduced remnants of the band of short rows of cilia reported in other species of the genus (Dauer 1987).

Remarks on Spatial and Temporal Occurrence.—The occurrence of *S. (S.) laciniata* in monthly samples from the two main study beaches that were investigated throughout the year (Patong Beach and Kata Beach) allows some preliminary observations on the life cycle of this species. These data will be treated in much greater detail in a forthcoming publication by Dexter.

The new species was found to be particularly abundant from July to October, i.e., during the height of the southwest monsoon season (Fig. 6). Within the beach zones of retention and resurgence, densities reached as high as 3,000 m^{-2} , whereas the average density of all 4 intertidal zones has been estimated to reach a maximum of 1,000 m^{-2} (D. Dexter, pers. comm.). Samples taken throughout this period contained large numbers of juveniles and sexually mature animals, indicating that reproduction may be more or less continuous at that time. Interestingly, samples from March also contained juveniles and mature adults, although in smaller numbers. The species abundance data suggest that *S. (S.) laciniata* has two annual spawning seasons.

Wave action is quite strong during the period in which *S. (S.) laciniata* "chooses"

Scolelepis (*Scolelepis*) *laciniata* n.sp.

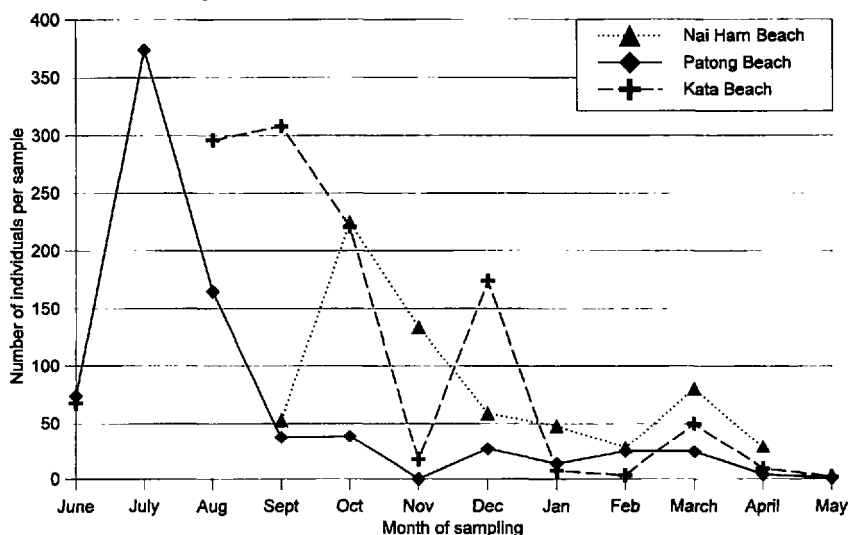


Figure 6. Graph illustrating seasonal fluctuation in occurrence of *Scolelepis* (*S.*) *laciniata* at three main study sites. The species is present in highest numbers during the SW monsoon (May to October). Each data point represents the total number of individuals found in 20 subsamples, each covering an area of 0.01 m².

to make its greatest reproductive effort. Curiously, this species occurred in greater numbers at Patong Beach (the type locality) than at Kata Beach, even though the former is more protected than the latter. The reason for this may be an increased ability of the larvae to settle under the less turbulent conditions at Patong Beach.

Another species of *Scolelepis* (*Scolelepis*) also occurred in great numbers in samples from the three beaches shown on the graph. It is probably undescribed and is here referred to as *S. (S.)* cf. *squamata* (O. F. Müller, 1806). To a certain degree, *S. (S.)* cf. *squamata* is the mirror image of *S. (S.) laciniata*, being present only in small numbers during the southwest monsoon but attaining densities as high as 1,500 m⁻² during the northeast monsoon (particularly from January to April).

As mentioned in the Materials and Methods, the sampling design used by Dexter involved the division of each beach into four zones according to the amount of water in the sand. After determining the number of individuals for each species within each zone, specimens of the same species were combined in the lab, irrespective of the zone in which they were collected. Unfortunately, during the original handling of the samples in Thailand, specimens of *S. (S.) laciniata* were combined with *S. (S.)* cf. *squamata*. Thus, the exact distribution of *S. (S.) laciniata* along the four study zones is not known. Judging from samples that essentially contained only this species, however, it would appear that it is most common in the zones of retention and resurgence.

ACKNOWLEDGMENTS

I am deeply grateful to D. M. Dexter (San Diego State University) for asking me to study her polychaete material from Thailand, for the obvious care she has taken in preserving the animals, and for sending great amounts of information on collection procedures, habitat parameters, and distribu-

tional details. The insightful comments of two anonymous reviewers allowed me to improve the clarity of this paper.

B. Rubæk and S. Elle (both ZMUC) are warmly thanked for providing the final versions of the drawings presented in this paper. N. L. Bruce (ZMUC) is thanked for the loan of his Zeiss Axioskop microscope.

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DATE ACCEPTED: May 21, 1996

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